15.—Fossil bandicoots (Marsupialia, Peramelidae) from Mammoth Cave, Western Australia, and their climatic implications

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Abstract

It is shown that the bandicoot genera *Isoodon* and *Perameles* are represented in fossil deposits from Mammoth Cave, Western Australia, but not *Macrotis* or *Chaeropus*. The abundance of *Perameles* relative to *Isoodon* appears to have declined markedly between the time of accumulation of the Mammoth Cave fossil deposits and the present. Some environmental change must be postulated for this decline, and such change may be dated as late Pleistocene. It is possible, but not proven, that the envirmonmental change may have been associated with an increase in rainfall.

Introduction

The occurrence of bandicoot remains among the fossils recovered early in this century from Mammoth Cave is reported by Woodward (1914); he lists *Thalacomys, Perameles* and *Isoodon,* but cites no specimens and provides no elaboration of his list. These three genera of bandicoots are listed by Bretnall, Chapman and Glauert (1926 p.70) again without elaboration. But later, Glauert (1948) lists *Macrotis* (= *Thalacomys*) and *Isoodon* but not *Perameles* from Mammoth Cave, still without elaboration. Later writers such as Lundelius (1960) have copied Glauert's 1948 list of bandicoots, and have made climatic inferences from the presence of *Macrotis* at Mammoth Cave (Cook 1960, Butler 1961). I have re-examined the bandicoot skull and mandible remains from Mammoth Cave and have compared them with modern specimens from the Western Australian Museum and other collections, cited below.

Modern bandicoots have been described by various writers, including Waterhouse (1846), Thomas (1888) Jones (1924) and Tate (1948). Numerous taxa have been proposed. I have followed Tate (1948) both in his nomenclature and in his taxonomic ranking of the bandicoots. It would appear that four genera of bandicoots have lived in the southern part of Western Australia within historic time, and should be considered as possibly occurring in the Mammoth Cave deposits; these four genera are *Perameles* Geoffroy 1803, *Isoodon* Desmarest 1817, *Macrotis* Reid 1837 and *Chaeropus* Ogilby 1838.

I have been able to examine one adult male skull and mandible of modern *Chaeropus* (Nat. Mus. Vict. C 470) and one juvenile (Aust. Mus. Syd. 422). To represent modern *Isoodon,* I have used only specimens of *I. obesulus* drawn from the well-watered south-western part of Western Australia. All Western Australian Museum specimens of modern *Perameles* and *Macrotis,* from whatever part of Western Australia or the Nullarbor region, and of whatever taxon recorded, have been used as examples of their respective genera, and in addition, I have examined modern specimens of *P. nasuta, P. fasciata, P. gunni* and one of *P. eremiana* from the collection of the National Museum of Victoria. Various fossil samples have also been examined—see Table 2. Raw data on the modern and fossil specimens used, including their museum catalogue numbers, have been lodged in the library of the Western Australian Museum.

My criteria for distinguishing one genus of modern Western Australian bandicoots from another are set out in Table 1. Attention has been concentrated on structures likely to be preserved in fossil bandicoot remains; in practice, mandibular characters are most useful, especially that listed last in Table 1. Figure 1 shows the difference in relationship between the coronoid process and the horizontal ramus of the mandible in modern *Perameles* and *Isoodon;* I have seen only two specimens of *Perameles*

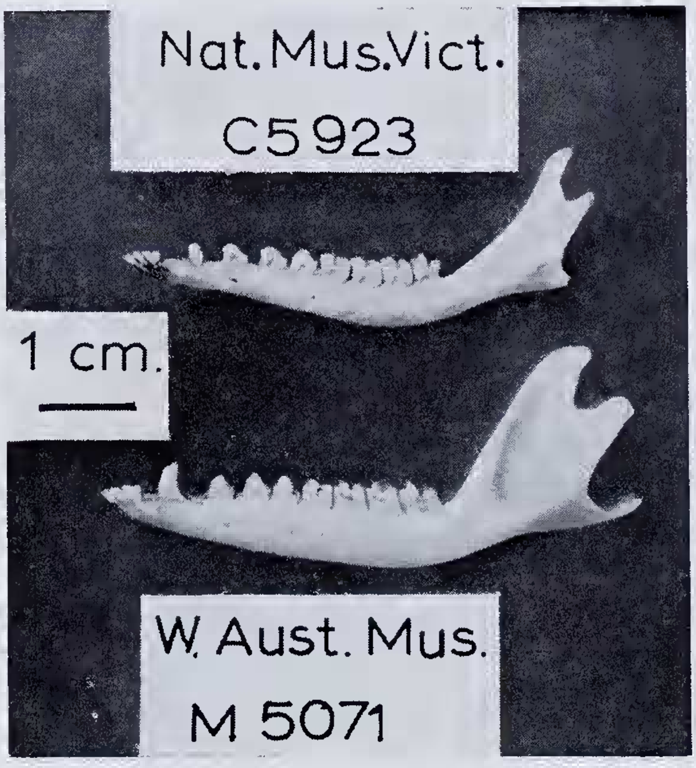

Figure 1.—Left mandibular rami, buccal view, of modern Victorian *Perameles fasciata* (above) and modern Western Australian *Isoodon obesulus* (below). Note smoothly curved junction of horizontal ramus with coronoid process in *Perameles*; contrast with obtuse angle in *Isoodon*.

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TABLE 1

Distinguishing features among genera of bandicoots living in Western Australia in historic time.

	Macrotis	*Isoodon*	*Perameles*	*Chaeropus*
Length relative to whole upper tooth row of I^1–I^5 diastema	small	small	large	negligible
Size of C^1 relative to P^1 in horizontal section	large	often very large, but may be comparable	comparable	comparable
Shape of M^1, M^2, M^3 in horizontal section	rounded blocks	rounded blocks	truncated triangles, tapering lingually	truncated triangles, somewhat tapering lingually
Shape of M^4 in horizontal section	length and width comparable	length and width comparable	length small, width great	length small, width great
Curvature in upper cheek tooth row	marked	slight (except *I. macrourus*)	slight	slight
Bulla	anterior portion large, ovoid to pyriform, posterior portion also inflated	large, pyriform	large, hemispherical to hemi-ellipsoidal	small, pyriform to hemiellipsoidal
Muzzle shape	markedly contracting in front of M^1	gently tapering towards front	tapering towards front	markedly contracting in front of M^1
Mandibular ramus below tooth row	robust	robust	slender	robust
Size of C_1 relative to P_1 in horizontal section	comparable	often very large, but may be comparable	comparable, or C_1 smaller	comparable
Length M_1–M_4	exceeds 18 mm.	less than 16 mm.	less than 16 mm.	less than 16 mm.
Shape of M_2 in horizontal section	width usually exceeds length	length usually exceeds width	length usually exceeds width	length exceeds width
Posteroventral border of mandible, vertically below coronoid process	marked, but relatively small buccal process	buccal crest	buccal crest	very marked, relatively large, slightly hooked buccal process
Junction of coronoid process with horizontal ramus of mandible	obtuse angle	obtuse angle	continuous smooth curve	obtuse angle

TABLE 2

Range of variation in dimensions of tooth alveoli in fossil and modern bandicoots. In millimetres.

Sample	Individuals in mandibular sample	Length I^1–M^4	Length M^1–M^4	Length x width M^4	Diastema I^4–I^5	Width C_1	Width P_1	Length x width P_3	Length x width P_4	Length M_1–M_4	Length x width M_2
Perameles— modern Victorian *P. fasciata*	2	35–36	11·6–11·9	1·8–1·9 x 3·0–3·3	1·9–2·4	0·6–0·9	0·7–0·8	2·7–3·2 x 0·7–0·9	2·7–3·0 x 1·1–1·4	12·6–12·7	3·1–3·2 x 2·3–2·4
Perameles— modern western *P. bougainvillei* group	11	31–35	9·3–11·1	1·3–1·9 x 2·8–3·3	1·0–2·1	0·5–0·9	0·6–1·0	2·7–3·2 x 0·7–1·0	2·5–3·1 x 1·0–1·4	11·1–12·1	2·6–3·1 x 1·8–2·2
Perameles— fossil, Mammoth Cave	12	....	....	....	....	0·9–1·5	0·7–1·2	3·0–3·8 x 0·9–1·2	2·6–3·5 x 1·0–1·5	12·3–13·9	2·9–3·6 x 1·3–2·3
Perameles— fossil, other caves in Augusta-Margaret River district	4	....	....	....	....	0·9–1·0	0·7–0·9	3·0–3·3 x 0·8–1·1	2·5–3·5 x 0·9–1·8	12·8–13·9	3·2–3·5 x 1·6–2·1
Perameles— fossil, caves in Nullarbor region	23	....	....	....	....	0·6–1·1	0·5–0·9	2·5–3·4 x 0·7–1·1	2·5–3·3 x 0·9–1·3	11·4–12·5	2·7–3·4 x 1·5–2·2
Perameles— fossil, caves c. 140 miles N of Perth	4	....	....	....	....	1·0	0·7–0·9	2·9–3·4 x 0·8–1·2	2·8–3·3 x 1·0–1·6	12·0–14·5	3·0–3·7 x 1·5–1·8
Perameles— modern Victorian *P. nasuta*	6	46–53	13·7–15·3	2·3–3·1 x 3·4–4·4	3·0–4·3	1·6–2·1	0·8–1·5	3·3–3·9 x 1·2–1·4	3·7–4·5 x 1·3–1·8	15·0–16·8	3·2–3·8 x 2·3–2·9
Perameles— modern Victorian *P. gunni*, from one locality	6	41–44	13·5–13·8	1·8–2·2 x 3·1–3·6	2·0–2·9	1·0–1·2	0·6–0·8	2·8–3·3 x 0·8–1·3	3·3–3·8 x 1·1–1·5	14·8–15·5	3·5–3·8 x 2·5–2·6
Isoodon obesulus— modern, south-western W.A.	30	34–42	11·7–13·8	2·5–3·7 x 2·9–4·2	0·5–1·2	1·0–2·8	0·9–1·7	2·6–3·4 x 1·0–1·7	2·4–3·5 x 1·3–2·2	13·6–15·9	2·5–4·1 x 2·6–3·4
Isoodon— fossil, Mammoth Cave	5	....	11·3	2·4–2·6 x 3·2	....	1·5–2·0	0·9–1·4	2·4–3·7 x 1·0–1·8	2·3–3·5 x 1·3–1·7	13·2–14·8	2·9–3·7 x 1·7–2·9
Macrotis— modern W.A. (mainly *M. lagotis*, with one specimen ascribed to *M. sagitta*)	26	48–63	16·4–19·5	3·7–5·3 x 3·6–6·6	0·2–1·6	1·3–2·7	1·1–1·8	4·3–6·1 x 1·1–2·1	3·7–4·8 x 1·6–2·5	18·4–22·3	3·9–5·5 x 4·2–6·6
Chaeropus— modern Victorian	1	35	11·8	1·5 x 3·8	0·2	0·7	0·9	2·8 x 1·0	1·8 x 1·2	13·6	3·1 x 2·8
Chaeropus— fossil, Nullarbor region	22	....	10·5–11·6	1·6–1·9 x 2·6–3·1	....	0·8–1·1	0·6–0·9	2·8–3·6 x 0·5–1·0	2·1–2·7 x 0·8–1·5	12·0–13·4	2·7–3·4 x 1·9–2·6

(both large male *P. nasuta*) in which confusion with other bandicoot genera would be at all likely in this character.

Lundelius (1960) mentions the location (in the extreme south west of Western Australia) and age (late Pleistocene) of the Mammoth Cave fossiliferous deposits.

The Mammoth Cave fossil bandicoots

By the criteria of Table 1, two kinds of bandicoots may be recognized among the Mammoth Cave fossils, *Perameles* and *Isoodon*. Specimens 66.2.178-193, 66.2.205-209, 66.3.101 and 66.7.12 (all mandibular fragments) represent *Perameles*. *Isoodon* is represented by 63.7.132 and 66.2.202 (parts of skulls), and by 66.2.194-201, 66.2.203, 66.2.204, and 66.2.210-215 (mandibular fragments). I have found no bandicoot specimen in the Mammoth Cave fossil collection of the Western Australian Museum which I could identify as *Macrotis*.

It would appear unlikely that any confusion of *Perameles* with *Macrotis* could arise, but large fragmentary specimens of *Isoodon* conceivably could be ascribed to *Macrotis*. Numerical data on *Perameles, Chaeropus, Macrotis* and *Isoodon*, both fossil and modern, have been assembled in Tables 2 and 3. Since the teeth are frequently missing from fossil bandicoot specimens, alveolar dimensions rather than actual tooth dimensions have been recorded. Measurements are recorded only from those fossil and modern specimens in which $P^1/_4$ and $M^4/_4$ appeared to be fully erupted and in use.

Table 2 shows that there is overlap in range of variation in some dimensions between the Mammoth Cave *Isoodon* sample and the modern *Macrotis* sample. In respect of width of alveoli of lower canines and of all three lower permanent premolars, the largest Mammoth Cave *Isoodon* exceeds the smallest modern *Macrotis*. In all other eight dimensions which can be compared, modern *Macrotis* exceeds Mammoth Cave *Isoodon*.

The modern sample of *Isoodon* differs most markedly from modern *Macrotis* in molar and canine dimensions. *Isoodon* may (but does not always) have conspicuously large canines, both upper and lower, far exceeding in relative and sometimes in absolute size, those of *Macrotis*. On the other hand, molar teeth in *Macrotis* usually greatly exceed those of *Isoodon* in absolute size. Table 2 shows some overlap in range of variation in the molar dimensions recorded for modern *Isoodon* and modern *Macrotis*, but the two genera are clearly separable on widths of the lower molars (exemplified by M_2 in Table 2) and by total length of the upper or lower molar rows. Table 2 shows that the fossil *Isoodon* sample from Mammoth Cave also differs markedly from modern *Macrotis*, without overlap in range, in widths of lower molars and in total length of upper and lower molar rows. In addition, modern *Macrotis* exceeds Mammoth Cave *Isoodon* in all other molar dimensions recorded in Table 2.

Only two individuals are represented by skulls in the Mammoth Cave fossil *Isoodon* sample. One of these (63.7.132) retains sufficient remnants of the bullae of both sides to show they conformed to the modern *Isoodon* bullar characteristics. Both 63.7.132 and the smaller fragment 66.2.202 show the muzzle shape at about the P^4-M^1 region, and it is not suddenly contracted in the manner characteristic of modern *Macrotis* and *Chaeropus*. Nor does the curvature of the molar row in 63.7.132 and 66.2.202 suggest *Macrotis* (or *Isoodon macrourus*) rather than *Isoodon obesulus*. Thus I am confident that no specimen from Mammoth Cave ascribed by me to *Isoodon* should really have been ascribed to *Macrotis*. I am also confident that specimens of *Chaeropus* have not been confused with *Isoodon*, because of the diagnostic differences set out in Table 1.

Individuals in the Mammoth Cave sample of *Perameles* tend to exceed those in the modern Western Australian sample in size, though there is overlap in range of variation for all those dimensions recorded in Table 2 except total length of the lower molar row; in this last dimension, the fossil sample from Mammoth Cave exceeds the modern *Perameles* sample absolutely, with means (see Table 3) differing significantly. It is possible, as Lundelius (1960) implies, that different species of *Perameles* are represented in these two samples.

Table 2 therefore lists other samples of *Perameles* drawn from the Western Australian Museum collection of fossil mammals. The age of these samples is not known, but all specimens except three appear to have been recovered from surface litter, not from excavations, in caves. Thus the specimens may be closer in average geological age to the modern specimens than to the Mammoth Cave fossil specimens recorded in Table 2. The Mammoth Cave fossils are not younger than 37,000 years B.P. (Lundelius 1960). Three samples of younger cave fossil specimens of *Perameles* are reported in Table 2, a small sample from caves not more than 20 miles from Mammoth Cave in the Augusta-Margaret River region, a small sample from caves about 140 miles north of Perth, and a larger sample from caves in the Nullarbor region.

If these younger cave fossil samples of *Perameles* be considered along with the modern western sample, and the whole composite sample compared with the older Mammoth Cave fossil sample, discrepancies between the younger and older samples still exist. Thus in width of C_1, P_1 and M_2, and length of P_3 some specimens of *Perameles* from Mammoth Cave exceed all other specimens available, though not greatly. In width of P_3, length and width of P_4, length of M_2 and length of M_1-M_4, range of variation in the combined younger samples of *Perameles* encompasses the range of variation shown by the older Mammoth Cave fossil sample. Neither the slight numerical discrepancies between these samples, nor any morphological considerations, demand that the Mammoth Cave specimens represent a different (larger) species of *Perameles* from the other specimens quoted. Table 2 also includes some samples of modern bandicoot species from eastern Australia. In those dimensions recorded in Table 2, there appear to be no closer resemblances between the Mammoth Cave fossil *Perameles* and modern eastern species than between Mammoth Cave fossil and modern western *Perameles*.

I have been able directly to compare cusp details in the fossil *Perameles* specimens with 15 modern specimens from Western Australia (ascribed to *P. myosura*, *P. eremiana* or *P. bougainvillei*) and with one specimen each of *P. fasciata* (Nat. Mus. Vict. C 5923 from the junction of the Murray and Darling Rivers) and *P. gunni* (Nat. Mus. Vict. C 1464 from Mt. Gellibrand, Victoria). In general, morphology of homologous teeth is very similar in all these modern specimens. However, neither Victorian specimen shows talonids as highly developed on P_1 or P_3 as do the modern Western Australian specimens, while C 1464 (*P. gunni*) differs from all the others in having a small cingular shelf on the antero-buccal aspect of M_1. In C 1464, each of the lower molars has such a shelf, that on M_1 being smaller than that on M_2, in turn smaller than that on M_3, in its turn smaller than that on M_4. C 5923 (*P. fasciata* from Victoria), M 2629 (*P. bougainvillei* from the Canning Stock Route, inland W.A.), and 10579 (*P. bougainvillei* from Dorre Island, W.A.) each shows a very small protruberance on the antero-buccal aspect of M_1, the other modern western Australian specimens showing a continuous smooth wall in this region; but a marked shelf is evident on the antero-buccal aspect of M_2 in all these modern specimens, a much larger shelf on M_3 and a much larger shelf still on M_4. C 1464 (*P. gunni*) differs from all the other modern specimens examined in exhibiting a smaller gradient of change in antero-buccal shelf size from M_1 to M_4.

Thus insofar as my comparisons show, the modern Western Australian species (one or more) of *Perameles* differ from modern eastern *P. fasciata* and *P. gunni* in having more marked talonids on the lower permanent premolars. The modern Western Australian species resembles *P. fasciata* and differs from *P. gunni* in showing a progression in antero-buccal shelf size from nil or nearly nil on M_1 to a very marked structure on M_4; *P. gunni* shows such a shelf on M_1, and progressively larger shelves on M_2, M_3 and M_4, but the gradient from before backwards is lower than in modern Western Australian species or in *P. fasciata*.

By these dental morphological criteria, available Western Australian fossil specimens agree with modern Western Australian species of *Perameles*. 27 fossil specimens of 29 showing some or all of P_1, P_3, M_1 and M_1-M_4 gradient agree completely with the modern Western Australian species. The other two fossil specimens (66.3.22 from about 140 miles north of Perth, and 66.1.56 from the Nullarbor region) have rather small talonids on the first two permanent premolars, different in degree but not in kind from the modern specimens.

Taken in conjunction with the size characteristics set out in Tables 2 and 3, these minor considerations of dental morphology suggest that neither the Mammoth Cave specimens of *Perameles*, nor any of the other Western Australian fossil *Perameles*, differ greatly from modern Western Australian *Perameles*. If one accepts the tentative suggestion of Tate (1948) that "the small bandicoots *P. bougainvillei*, (including *myosura*, D. M.), *fasciata*, *notina* and *eremiana* may be local races of a single widespread southern species . . .", then all the Western Australian fossil *Perameles* specimens cited above may be included in this species. Tate (1948) adopts the cautious concept of a "*Perameles bougainvillei* group" to cover his uncertain taxonomic situation, and I refer all the Western Australian fossil specimens cited above of *Perameles* to a "*P. bougainvillei* group" in Tate's meaning.

Climatic implications of the Mammoth Cave fossil bandicoots.

As noted above, inference of drier climatic conditions has been drawn from the supposed presence of *Macrotis* in the Mammoth Cave deposits. Since there is no *Macrotis* present, this climatic inference cannot now be entertained. In any case, the correlation of *Macrotis* with dry climate may not be very close. *M. lagotis* appears to be a very wide-ranging species. The Western Australian Museum collection includes modern specimens from Bridgetown, with a mean annual rainfall in excess of 30 inches, Cranbrook (over 20 inches) and other well-watered localities, as well as localities like Cue (less than 10 inches mean annual rainfall) which could be described as very dry. Species of *Macrotis* other than *lagotis*, however, would appear to be confined to very dry regions, according to the locality data supplied by Jones (1924).

If Tate (1948) is right in recognising *Isoodon obesulus* as a very wide-ranging species which includes the race *auratus*, then *Isoodon obesulus* can hardly be taken as an index of climate. The Western Australian Museum collection includes modern specimens of *Isoodon obesulus* (in Tate's sense) from Cowaramup (mean annual rainfall exceeding 40 inches) and from Lake Tobin (mean annual rainfall less than 10 inches, and very unreliable). The Cowaramup specimen (M 4522) demonstrates that *Isoodon* still survives in the neighbourhood of Mammoth Cave. The presence of *Isoodon* in the Mammoth Cave fossil deposit therefore carries no implication of a change in climate.

No specimen of *Chaeropus*, fossil or modern, from the vicinity of Mammoth Cave is known to me, though there is a record from the nearby Lake Cave of footprints, presumably modern, attributed to *Chaeropus castanotis* (E. A. Le Souef, 1905, reported in "The West Australian" 21st February, 1914.)

Perameles appears not to have lived in the Mammoth Cave region in historic time. There is no modern specimen of *Perameles* from the Cape Naturaliste-Cape Leeuwin region (extreme south-west of Western Australia) in the Western Australian Museum collection, and all the specimens in this collection suggest that the "*Perameles bougainvillei* group" represents rather dry, if not very dry, climatic conditions,

TABLE 3

Statistical summary of some alveolar dimensions in selected samples of fossil and modern bandicoot mandibles.

(Sex differences listed for *Macrotis* and *Isoodon*, and difference in M_1-M_4 length between modern western and Mammoth Cave fossil *Perameles*, are significant on student's t test.)

Sample	Dimension examined	No. of specimens	Observed range mm.	Mean mm.	Standard deviation mm.	Coefficient of variation
(From Western Australian Museum collections with exception noted below)						
Macrotis lagotis—modern, both sexes included, from many Western Australian localities	Width M_2	23	4·2– 6·6	5·2	0·65	12·5
—same sample, males only	Length M_1–M_4	13	19·5–22·3	21·1	0·92	4·4
—same sample, females only	Length M_1–M_4	11	18·4–21·4	19·9	0·97	4·9
Isoodon obesulus—modern, both sexes included, from South West Division of Western Australia	Width M_2	31	2·4– 3·4	2·9	0·19	6·6
—same sample, known males only	Length M_1–M_4	15	13·6–15·9	15·3	0·61	4·0
—same sample, known females only	Length M_1–M_4	8	12·9 15·1	14·3	0·69	4·8
—same sample, known males only	Width C_1	15	1·6– 2·8	2·2	0·34	15·6
—same sample, known females only	Width C_1	8	1·0– 1·3	1·2	0·12	9·8
Mammoth Cave fossil *Isoodon*	Length M_1–M_4	4	13·5 14·8	14·2	0·61	4·2
	Width M_2	5	2·4– 2·9	2·7	0·21	7·6
Perameles bougainvillei group—modern, both sexes included, from several widely separated Western Australian and Nullarbor localities	Length M_1–M_4	11	11·1–12·1	11·7	0·36	3·1
	Width M_2	11	1·8– 2·2	2·0	0·15	7·3
Mammoth Cave fossil *Perameles*	Length M_1–M_4	10	12·7–13·5	13·2	0·26	2·0
	Width M_2	12	1·6– 2·1	1·9	0·19	10·1
Other Augusta-Margaret River cave fossil *Perameles*	Length M_1–M_4	4	12·8–13·9	13·3	0·46	3·4
	Width M_2	4	1·6– 2·1	1·8	0·19	10·4
Nullarbor cave fossil *Perameles*....	Length M_1–M_4	22	11·4–12·5	12·0	0·32	2·7
	Width M_2	23	1·5– 2·2	1·7	0·19	11·2
Perameles gunni—modern, National Museum of Victoria specimens, both sexes included, from Mt. Gellibrand, Vic.	Length M_1–M_4	6	14·8–15·5	15·1	0·26	1·7
	Width M_2	6	2·5– 2·6	2·5	0·04	1·6
Nullarbor cave fossil *Chaeropus*	Length M_1–M_4	22	12·0–13·4	12·7	0·34	2·7
	Width M_2	22	1·9– 2·6	2·2	0·21	9·4

though Glauert (1950) mentions a record of *Perameles* from the Albany region, most of which could be described as well-watered. The possibility should be considered that the presence of *Perameles* in the Mammoth Cave fossiliferous deposit indicates drier climatic conditions at the time of accumulation of this deposit than at present.

Not only was *Perameles* present at the time of accumulation of the Mammoth Cave deposit, but also it appears to have been the more abundant of the two kinds of bandicoots present. At least 13 individuals of *Perameles* are represented in the Mammoth Cave deposit as against 8 individuals of *Isoodon*. The Mammoth Cave deposits appears to me to have been a talus deposit, probably accumulating through holes in the cave roof. Thus it is probable that the animals represented in it fell involuntarily to their deaths. It is correspondingly improbable that the difference in representation of *Perameles* and *Isoodon* is due to *Perameles* being a cave-haunting and *Isoodon* a cave-avoiding form. Nor is it probable that *Perameles* suffered predation by a carnivore preferentially to *Isoodon*. The carnivores *Thylacinus, Sarcophilus, Thylacoleo* and even *Dasyurus,* which might have been bandicoot-eaters, have been reported from the Mammoth Cave deposit (Glauert 1948), but I know of nothing to suggest that the deposit was accumulated by these carnivores and that they were not the victims of falling through a hole in the cave roof equally with the other mammals represented in the deposit. It is simpler to postulate that the greater representation of *Perameles* than of *Isoodon* in the Mammoth Cave deposit reflects a larger population of *Perameles* than of *Isoodon* in the vicinity of the cave when the deposit was being accumulated. The deposit does not appear to be an owl pellet accumulation.

If *Perameles* (of the *bougainvillei* group) was once the commoner bandicoot in the Mammoth Cave region but does not now live there, whereas *Isoodon obesulus* was and still is present, it would appear reasonable to postulate some major environmental difference between the present time and the time of accumulation of the Mammoth Cave deposit. If the *Perameles bougainvillei* group represents drier climatic conditions, whereas *Isoodon obesulus* shows wide climatic tolerance, the major environmental change may well have been climatic; the climate may have been drier when the Mammoth Cave deposit was being accumulated than it is now. However, the ecological requirements of bandicoots appear not to have received extensive study, so that it would be rash to press this climatic supposition too far; other ecological factors than macro-climatic may have influenced the observed change.

Lundelius (1957) has shown from a study of superficial deposits in caves that *Perameles* has been more widely distributed in past, but not remote, time than at present. Elsewhere (Lundelius 1960) he has recorded *Perameles* at about 8,500 years B.P. and at about 12,000 years B.P. from shallow deposits in (an antechamber to) Nannup Cave, about 8 miles south of Mammoth Cave; *Isoodon* is also recorded from these same "Nannup Cave" deposits.

The Western Australian Museum collection of fossil mammals includes specimens from the Nannup Cave antechamber and from two other caves in the same (extreme south-western) region as Mammouth Cave, representing a total of 4 individuals of *Perameles*. Many more caves in this region have yielded many more individuals (at least 38) of *Isoodon*. As noted above, most of these specimens of *Isoodon* and at least one (66.2.53) of the few *Perameles* specimens in the Western Australian Museum fossil collection come from surface deposits within caves, whereas the Mammoth Cave specimens come from beneath a flowstone layer (Glauert 1910). These more superficial deposits presumably represent more recent times than the Mammoth Cave deposit.

Thus it would appear that the decline and ultimate extinction of *Perameles* in the Mammoth Cave region resulted from a slow trend rather than from a catastrophic change, and that this trend became evident at some time after the accumulation of the (buried) Mammoth Cave deposits but before the unknown but presumably relatively recent time of accumulation of most of the superficial south-western cave deposits. *Perameles* was abundant (relative to *Isoodon*) in the Mammoth Cave region over 37,000 years ago, was still present 8,500 years ago, and although in smaller proportion, was probably present still later, but not up to historic time. The environmental change which must be postulated to account for the relative decline in *Perameles* in the extreme south-west of Western Australia presumably therefore began in late Pleistocene time. This change may have been macro-climatic, and if so, is likely to have been one of increasing rainfall.

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Note added in press: G. E. Heinsohn (1966, *University of California Publications in Zoology* 80) reports ecological studies on *Perameles gunni* and *Isoodon obesulus* in north western Tasmania. These species occur together, eat similar food (mainly earthworms and insect larvae) and in other ways are similar, but *Isoodon* remains within a vegetation cover whereas *Perameles* forages in open areas. On this analogy, the late Quaternary increases in *Isoodon* obesulus relative to *Perameles* cf. *bougainvillei* in the Cape Naturaliste—Cape Leeuwin region, Western Australia may reflect an increasing density of low-growing vegetation or a reduction in open spaces. L. Freedman (1967, *Records of the Australian Museum* 27: 147-165) and L. Freedman and A. D. Jaffe (1967, *Records of the Australian Museum,* 27: 183-212) describe and illustrate skull and tooth characters in *Perameles.* Freedman (1967) cites "*P. gunnii*" and "*P. bouganville*" as the original spellings.